

Macrofungi can be assessed directly in the field, with checking where necessary in the laboratory. Microfungi can be separated under the microscope, while fungi are isolated from microhabitats onto artificial media and then can be separated by their characters. The use of fungi in future environmental impact assessment is a real option.

For background information see FUNGI; MYCORRHIZAE in the McGraw-Hill Encyclopedia of Science & Technology. Kevin D. Hyde

Bibliography. K. D. Hyde, *Biodiversity of Tropical Microfungi*, Hong Kong University Press, 1997; K. D. Hyde, Can we rapidly measure fungal diversity?, *Mycologist*, 11:176-178, 1997; B. Kendrick, *The Fifth Kingdom*, Mycologue Publications, 1992; S. B. Pointing and K. D. Hyde, *Bioexploitation of Fungi*, Fungal Diversity Research Series 2, Hong Kong, 2000.

## Fungi

Mycorrhizal fungi are ecologically significant because they form symbiotic relationships in and on the roots of host plants. The host plant provides the fungus with a soluble carbon source, and the fungus provides the host plant with an increased capacity to absorb water and nutrients from the soil. Thus, both partners benefit from this relationship. It has been found that the majority of plants do have mycorrhizal fungi associated with them; some of these associations are very specific while others are very broad.

Mycorrhizal fungi are classified into four major types: ectomycorrhizal, arbuscular mycorrhizal, ericaceous mycorrhizal, and orchid mycorrhizal. (see *illus.* and *table*) Ectomycorrhizal fungi are

characterized by the presence of a Hartig net and a fungal sheath, and the absence of fungal hyphae in the plant root cells. The Hartig net is a complex network of fungal hyphae that penetrates between the root cells but does not penetrate into the root cells. Nutrient exchange between the fungus and the host plant occurs at the Hartig net. The fungal sheath is a compact layer of fungal hyphae, with varying thickness depending on the specific fungus, that surrounds the young root surface of the host plant. The fungal sheath prevents direct contact between the root and the soil. The fungal sheath serves as a nutrient reservoir and also provides protection from pathogenic microorganisms for the host plant.

Arbuscular mycorrhizal fungi are characterized by the presence of fungal hyphae within the root cells, the absence of a Hartig net, and the presence of fungal hyphae on the root surface but not as a fungal sheath. The arbuscules are branched hyphae found inside the root cells, and this is the area of nutrient exchange between the fungus and the host plant.

Ericaceous mycorrhizal fungi form symbiotic associations with plants in the Ericaceae family. They are divided into three subgroups which are characterized by the presence or absence of a Hartig net, a fungal sheath, and fungal hyphae within the root cells.

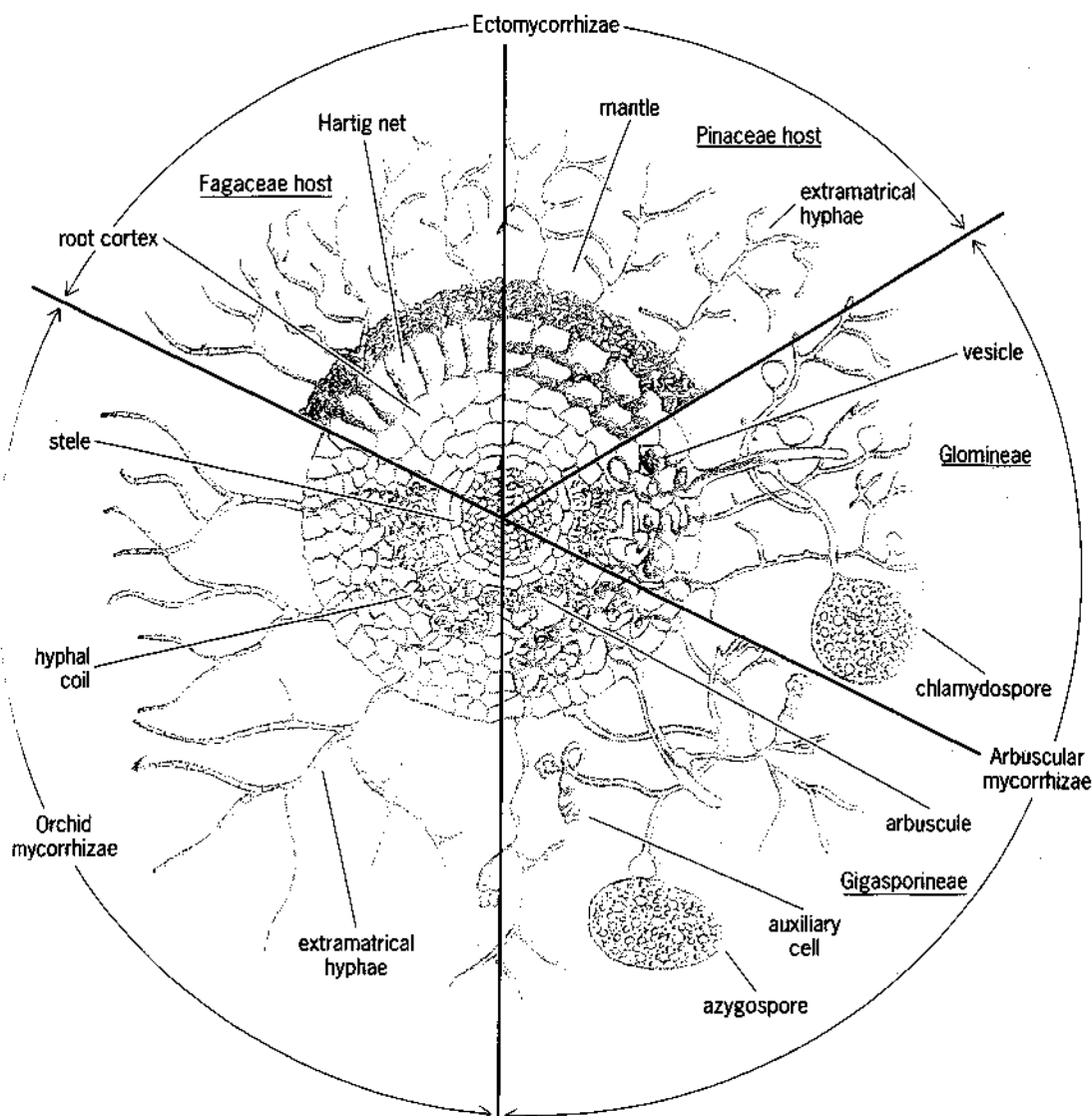
Orchid mycorrhizal fungi are characterized by the absence of a Hartig net and a fungal sheath and the presence of hyphal coils in the root cells. This type of fungus-host plant relationship is actually more parasitic than symbiotic in the early stages of plant growth because as a seedling the orchid is totally dependent on the fungus for growth.

Numerous studies have shown the important benefits of the fungus-host plant relationship for the plant in terms of water and nutrient uptake.

Plant host, fungi, and important characteristics of major types of mycorrhiza\*

Mycorrhizal type	Hosts involved	Fungi involved	Characteristic structures	Characteristic functions
Ectomycorrhizal	Mostly gymnosperms Some angiosperms Restricted to woody plants	Mostly basidiomycetes Some ascomycetes Few zygomycetes	Hartig net Mantle Rhizomorphs	Nutrient uptake Mineralization of organic matter Soil aggregation
Arbuscular	Bryophytes Pteridophytes Some gymnosperms Many angiosperms	Zygomycetes (Glomales)	Arbuscules Vesicles Auxiliary cells	Nutrient uptake Soil aggregation
Ericaceous	Ericales Monotropaceae	Ascomycetes Basidiomycetes	Some with hyphae in cell, some with mantle and net	Mineralization of organic matter Transfer between plants
Orchidaceous	Orchidaceae	Basidiomycetes	Hyphal coils	Supply carbon and vitamins to embryo
Ectendomycorrhizal	Mostly gymnosperms	Ascomycetes	Hartig net with some cell penetration Thin mantle	Nutrient uptake Mineralization of organic matter

\*From D. M. Sylvia et al. (eds.), *Principles and Applications of Soil Microbiology*, Prentice Hall, 1998.



Cross section of several types of mycorrhizal fungi. (Modified from original drawing by V. Furlan; used with permission)

Mycorrhizae greatly increase the total volume of soil which is now available for nutrient and water uptake, by increasing the root surface area for absorption of water and nutrients. Because the fungal hyphae can penetrate areas of the soil not available to the plant roots, it can access water and nutrients, especially phosphorus, that would otherwise be unavailable to the plant. This is especially noticeable in a stressed environment. In arid climates or nutrient-deficient soils, this capability often makes the difference between plant survival or death.

The uptake of nutrients by the mycorrhizal fungi is affected by the same conditions that affect uptake by the root, such as temperature and oxygen. Nutrients known to be absorbed by mycorrhizal fungi include phosphorus, nitrogen, potassium, copper, zinc, and sulfur. These nutrients often exist in low concentrations or have low mobility in the soil. The most dramatic example of increased mineral uptake by mycorrhizal fungi is with phosphorus. In a phosphorus-deficient soil, uninfected plants grow quite poorly.

However, if the plant is infected with mycorrhizal fungi, there is good, healthy, normal plant growth despite low concentrations of soil phosphorus. Sometimes phosphorus is present in a soil but not in a form available to the plant, or it is adsorbed to the soil particles. The sources of phosphate available to the mycorrhizal fungi are inorganic orthophosphate and phytate. The mycorrhizal fungi are capable of utilizing or degrading organic matter to obtain phosphorus which is unavailable to plant roots; one example is the organic phosphorus source, phytate. After the mycorrhizal fungus has decomposed the phytate, phosphorus is absorbed, and is translocated by cytoplasmic streaming to the plant root. In the mycelial strands a large portion of the phosphorus exists as polyphosphate, which can be stored and later translocated to the root via cytoplasmic streaming.

Increased nitrogen uptake, especially in the form of ammonium, has also been observed with mycorrhizae. Mycorrhizal fungi are able to utilize insoluble

organic nitrogen compounds found in humus. Once nitrogen is taken up by mycorrhizae, it is converted to glutamine in the fungal hyphae and is then transferred to the host plant. Nitrogen and phosphorus metabolism are closely interrelated, and the increase in nitrogen uptake in mycorrhizal plants may actually be an indirect effect of the increased phosphorus uptake.

Carbon flows from plant leaves to roots in the form of sucrose produced via photosynthesis, and it is then transferred to the mycorrhizal fungus. In arbuscular mycorrhizal fungi, the plant carbon is converted to glycolipids by the fungus, which allows for the accumulation of carbon by the fungus. In ectomycorrhizal fungi, the plant carbon is converted by the fungus to carbohydrates that the plant cannot utilize and is stored in the fungal sheath. This provides the fungus with a carbon concentration gradient in its favor. Studies have found trehalose, mannitol, and glycogen present in ectomycorrhizal roots but absent in uninfected roots. Mannitol and trehalose are known to be utilized by ectomycorrhizal roots but not by uninfected roots. Sucrose from the host plant is translocated to the roots, where the ectomycorrhizal fungus converts it to glucose and fructose. These two types of carbohydrates are then transferred to the fungal sheath, where the glucose is converted to glycogen and trehalose and the fructose is converted to mannitol. Studies have shown that the majority of the carbon received from the host plant by the fungus is used as an energy source for nutrient uptake instead of for fungal growth. If most of the carbon was used for fungal growth, the fungus would not be able to continue in its role of nutrient uptake in this symbiotic relationship with the plant.

Studies have also shown that plants with mycorrhizal fungi associated with their roots have an extra form of protection against toxins in the soil, root pathogens in the soil, and pH and temperature extremes. Because the fungal sheath prevents direct contact between the soil and the root, it allows the plant to survive in soil conditions which may be harmful to the plant alone.

Mycorrhizal fungi play a large role in helping to maintain a balance within an ecosystem. Because the fungal hyphae extend throughout the soil, they help to improve the soil structure by increasing aeration and moisture infiltration. They are also involved with various nutrient cycles, including carbon, phosphorus, and nitrogen. Mycorrhizal fungi provide a direct link between soil nutrients and plants by providing the host plant with nutrients otherwise not available. These fungi also have an effect on the decomposition of organic matter in soils. This may be due to the competition between the mycorrhizal fungi and the decomposers for limiting nutrients such as nitrogen. Some ectomycorrhizal fungi have been shown to obtain energy and nutrients by degrading organic materials in soil, thereby living independently of a host plant.

Some fungi, especially the ectomycorrhizal and ericaceous mycorrhizal fungi, may not be as depen-

dent on the host plant as previously thought. Mycorrhizal fungi do possess a wide variety of enzymes which would account for their ability to utilize other carbon sources. Mycorrhizal fungi long have been studied for their ecological benefits to the plant. Because many plants cannot survive without this relationship with the fungus, most emphasis was put toward how to improve the plant's growth. More recently the emphasis has been moving toward the capabilities of the fungus itself. Mycorrhizal fungi have been studied for applications in phytoremediation of toxic organic chemicals, heavy metals, and radionuclides in contaminated soils.

For background information see ERICALES; FOREST ECOSYSTEM; FUNGAL BIOTECHNOLOGY; FUNGAL ECOLOGY; FUNGI; MYCORRHIZAE; RHIZOSPHERE; ROOT (BOTANY) in the McGraw-Hill Encyclopedia of Science & Technology.

Paula Donnelly Nellessen; James A. Entry

Bibliography. M. E. Allen, *The Ecology of Mycorrhizae*, Cambridge University Press, Cambridge, 1991; J. L. Harley, The significance of mycorrhizae, *Mycol. Res.*, 92:129-139, 1989; S. E. Smith and D. J. Read, *Mycorrhizal Symbiosis*, Academic Press, San Diego, 1997; D. M. Sylvia, Mycorrhizal symbioses, in D. M. Sylvia et al. (eds.), *Principles and Applications of Soil Microbiology*, Prentice Hall, Upper Saddle River, NJ, 1998.

## Fungi (medicine)

Many medicines in use today are derived from compounds originally produced by fungi. A number of modern drugs are the purified form of chemicals present in traditional medicines, but only a few macrofungi, such as *Cordyceps sinensis*, which grows on caterpillars of the moth *Hepitis fabricius*, have been used in traditional medicines. However, since the 1940s the pharmaceutical industry has relied upon microfungi as sources of new medicines. Of the current top-selling prescription medicines, pravastatin, simvastatin, and lovastatin (all used to lower plasma lipoprotein levels) are derived from a molecule, mevinolin, produced by *Aspergillus terreus*. Three other top-selling medicines derived from fungi include the antibacterial antibiotics amoxicillin (a semisynthetic penicillin which is sold in combination with another compound) and ceftriaxone (a cephalosporin), and the immunosuppressive agent cyclosporin.

**Secondary metabolites (natural products).** Fungi growing in natural environments utilize surrounding nutrients and extract energy for conversion into biomass using primary metabolism. So-called secondary metabolites are often produced during growth and, more especially, as growth slows during nutrient depletion. The role of these metabolites in the producing organism is not entirely clear, but it is argued that fungi have evolved the ability to biosynthesize secondary metabolites due to the selectional advantages they obtain as a result